

ON THE TAXONOMIC STATUS, DISTRIBUTION AND ECOLOGY OF
THE BLUE ANTELOPE, *HIPPOTRAGUS LEUCOPHAEUS*
(PALLAS, 1766)

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(With 2 figures, 1 map and 3 tables)

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INTRODUCTION

The first published account of the blue antelope was made by the German Peter Kolb (1719 as cited in Mohr 1967: 6-10) who lived and travelled in what is now known as the south-western and southern Cape between 1705 and 1712. Subsequently, other nineteenth-century visitors to the Cape published independent descriptions of this creature, which they encountered just east of the Hottentots-Holland Mountains, mainly in the triangle Swellendam-Caledon-Bredasdorp but occasionally as far east as Plettenberg Bay. On the basis of skins and skulls sent back to Europe, Pallas (1766 as cited in Mohr 1967: 11) presented the first truly systematic description of the species, which he called *Antilope leucophaea*. In 1774 Thunberg reported that the blue antelope had become very uncommon (Mohr 1967: 6). The last one was seen around 1800, making this species the first historically recorded African mammal to become extinct (Harper 1945: 698-700).

The early extinction of the blue antelope, before qualified scientists could observe wild or even captive specimens, left open many questions concerning its

physical appearance, taxonomic status, geographic distribution, and ecology. There are, of course, no photographs, and most of the available sketches and descriptions are obviously inaccurate in one respect or another. Kolb, for example, drew the creature with a beard, apparently because he thought it was a close relative of the goats (he placed the blue antelope in the genus *Capra*) and some subsequent writers followed this custom. From Mohr's (1967) review of the early drawings and descriptions, it is apparent that they often contradict one another and are also at variance with the four mounted specimens still available in Europe, as well as with what may be surmised about the blue antelope from knowledge of its closest living relatives, the roan (*Hippotragus equinus*) and the sable (*H. niger*).

In her monographic study of the blue antelope, Mohr (1967) was forced to rely heavily on the mounted specimens (one each in Vienna, Stockholm, Paris, and Leiden) and on a skull housed in the Hunterian Museum at the University of Glasgow. This skull has no history attached to it, but Broom (1949) assigned it to *H. leucophaeus*, mainly because there was reason to believe it had been obtained before 1800—a time when the blue antelope was the only species of *Hippotragus* that had been encountered by Europeans (according to Broom, *H. equinus* was first seen by Europeans in 1804, *H. niger* in 1836). In the few years since Mohr's monograph was completed, a considerable amount of relevant osteological material has been found at archaeological and palaeontological localities in or near the area where *H. leucophaeus* was recorded historically. The purpose of this paper is to summarize the taxonomic, distributional, and ecological implications of this material.

DEFINITION OF THE SAMPLES

The initial stimulus for this paper was the observation that teeth assignable to the genus *Hippotragus* from the archaeological site of Nelson Bay Cave (Plettenberg Bay) were remarkably variable in size (Fig. 1), being sometimes significantly smaller and sometimes appreciably larger than homologous teeth of the largest *H. equinus* specimen in the South African Museum's comparative collection. Nelson Bay Cave lies within the historic area of distribution of *H. leucophaeus*, and it seemed highly probable that it would be represented at the site. With this in mind, two explanations of the observed size variation in Nelson Bay *Hippotragus* teeth seemed possible: (1) All the Nelson Bay teeth derived from *H. leucophaeus*, which was highly variable in size and which, contrary to historic observations, included some individuals as large or larger than the living roan; (2) the Nelson Bay sample included teeth from *H. leucophaeus* and

also from another species of *Hippotragus*, perhaps *H. equinus*.¹ In order to determine which hypothesis was more likely and possibly at the same time establish some of the metrical characteristics of *H. leucophaeus* vs. those of *H. equinus* and *H. niger*, it was obviously necessary to obtain measurements on samples of well-defined *H. equinus* and *H. niger* and also on fossil *Hippotragus* from other southern Cape sites.

A list of the relevant fossil sites with some background data on each is presented in Table 1. Map 1 gives their locations. At most of the sites, analysable *Hippotragus* remains consist overwhelmingly of isolated teeth. Whole dentitions are common only from Swartklip and even there the number is not large. Three sites have provided analysable horn cores (an example from Nelson Bay Cave is illustrated in Fig. 2). No complete or even nearly complete skulls are known. Post-cranial remains occur at several sites, but have been ignored here because: (1) they are exceedingly difficult to distinguish from the post-cranial bones of other similar-sized bovid genera represented in the same collections; (2) most of the post-cranial material is highly fragmentary, greatly reducing its descriptive and analytic value (and compounding the difficulty of generic identification); and (3) there are no large museum samples of well-identified recent *Hippotragus* post-cranial remains with which to compare the fossil material. Data on the quantities of analysable teeth and horn cores available from the different sites are presented in Appendix 1.

The recent samples of *H. equinus* and *H. niger* with which the fossil material is compared are composites of collections housed in the South African Museum (Cape Town), the Transvaal Museum (Pretoria), the National Museum of Rhodesia (Bulawayo), the British Museum (Natural History) (London) and the Field Museum of Natural History (Chicago). The geographic provenances of the samples are given in Table 2, from which it can be seen that specimens from south-central Africa (especially Zambia) predominate heavily in both samples, giving them a distinct geographic bias. There are two few well-provenanced specimens from other areas in either the *H. equinus* or the *H. niger* sample to say with any certainty that geographic differences in size do not characterize either or both species, but the data are sufficient to argue that any differences which do exist are probably small. Further, my search of the literature has failed to turn up any references to marked size differences among recognized subspecies of either *H. equinus* or *H. niger*, with the exception of *H. niger variani*, the 'giant sable' of Angola. I encountered only one *H. niger variani* specimen in the museum collections I examined (in the Field Museum) and measurements on it were recorded separately from those of the remaining *H. niger* sample. I think it is fair to conclude that the admitted geographic bias of the two comparative samples does not disqualify them for use in this study.

¹ The possibility that the second species might be the extinct giant hippotragine, *Hippotragus gigas*, was ruled out since the relevant Nelson Bay teeth were all morphologically quite distinct from teeth of *H. gigas*, as known, for example, from Elandsfontein. The dentition of *H. gigas*, in fact, is morphologically more like that of recent *Oryx* spp. (though much larger) than that of recent *Hippotragus* spp.

Table 1
Southern Cape palaeontological and archaeological sites from which the *Hippotragus* remains analysed in this paper were derived.

Site	Bone accumulation related to human activity?	Geological age of <i>Hippotragus</i> fossils (and nature of supporting evidence) ^a	Reference		Present location of material
Elands Bay Cave	Yes	11 000 to shortly after 9 600 B.P. (C-14)	Parkington (1972); Klein (unpubl.)	Department of Archaeology, University of Cape Town	South African Museum
Elandsfontein	Probably at least in part	Middle and Upper Pleistocene (palaeontological inference) ^b	Hendey (1969, 1974); Klein (1974)	South African Museum	South African Museum
Bloembos	Possibly	?Upper Pleistocene (palaeontological inference)	Cooke (1947); Hendey (1974)	South African Museum	South African Museum
Eyre's Cave	Probably	Later Last Glacial and Holocene (palaeontological and archaeological inference)	Klein (1974)	South African Museum	South African Museum
Hawston	Probably	?Holocene (no provenance data)	None	South African Museum	South African Museum
Oakhurst	Yes	Terminal Last Glacial and Holocene (archaeological inference)	Goodwin <i>et al.</i> (1938); Wells (1960)	South African Museum	South African Museum
Lake Pleasant (Groenvlei)	No	?Later Last Glacial (geological inference)	Butzer & Helgren (1972)	South African Museum	South African Museum
Nelson Bay Cave	Yes	18 500-5 000 B.P. (C-14) ^c	Klein (1972a, b, 1974)	South African Museum	South African Museum
Swartklip	No	>40 000 years B.P. ^d ; earlier Last Glacial (C-14 and geological inference)	Hendey & Hendey (1968); Butzer (in press)	South African Museum	South African Museum
Klaies River Mouth Caves	Yes	Between > 30 000 B.P. and the end of the Last Interglacial (C-14 and geological inference)	Wymer & Singer (1972) and in press; Klein (1974)	South African Museum	South African Museum
Craddock Springs	Probably	Earlier Last Glacial (archaeological inference)	Wells (1970); Klein (1974)	Port Elizabeth Museum	Port Elizabeth Museum
Melkshoutboom	Yes	15 400 to shortly before 7 600 B.P. (C-14)	Deacon (1969, 1972)	Department of Archaeology, University of Stellenbosch	Department of Archaeology, University of Stellenbosch
Uiondale Shelter	Yes	Holocene (archaeological inference)	M. Brooker (pers. comm.)	Albany Museum (Grahamstown)	Albany Museum (Grahamstown)

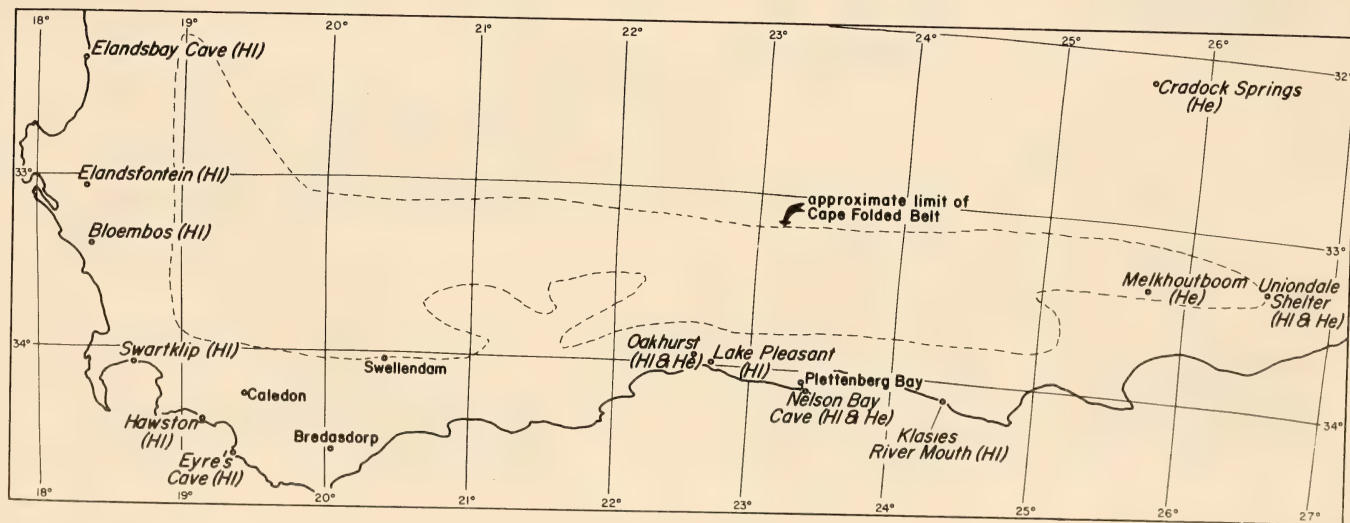
NOTES:

^a The term Upper Pleistocene is used here to refer to the combined time-span of the Last (Eem) Interglacial and the Last (Würm) Glacial, or in absolute terms, roughly the time interval from 125 000 B.P. to 10 000 B.P. The Last Interglacial/Last Glacial boundary probably falls in the interval 75 000–70 000 B.P.

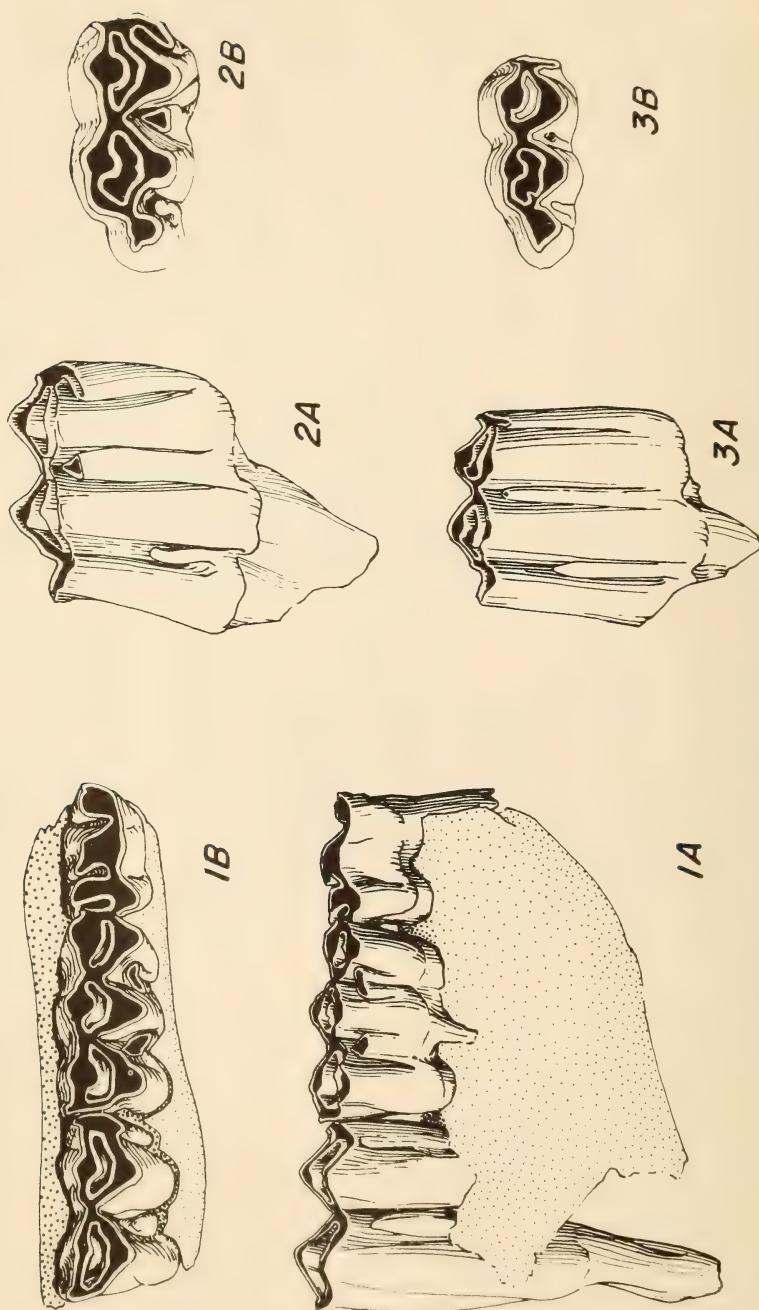
^b Most of the Elandsfontein faunal material has been collected from one or more calcareous or ferruginous palaeosurfaces exposed during recent deflation of overlying sands. The bulk of the fauna probably dates from the Middle Pleistocene (Klein 1974), but a portion, including perhaps bones assigned to *H. leucophaeus*, may be considerably younger.

^c Inskeep has excavated deposits at Nelson Bay that are younger than 5 000 B.P. These may also contain hippotragine remains, but the mamalian fauna from them has not yet been analysed.

^d A single C-14 date of >40 000 years. (I-6840) (Buckley, pers. comm.) has been obtained on ostrich eggshell in direct association with mammal bones at Swartklip.



Map. 1. Southern Cape localities mentioned in the text (HI, He—locality contains bones assigned to *Hippotragus leucophaeus* or *H. equinus* respectively).



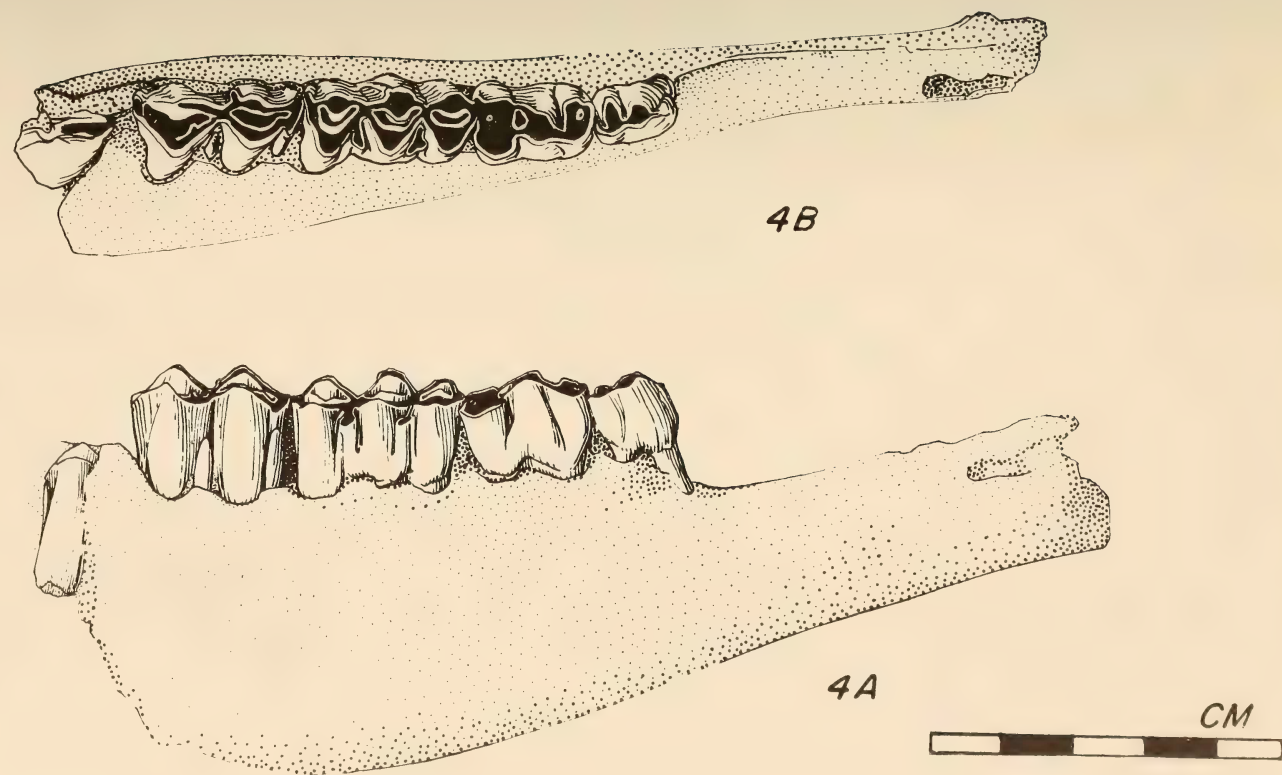


Fig. 1. 1A, 1B: dP_3 (MW), dP_4 (MW), M_1 (EW) of *Hippotragus equinus* from Nelson Bay Cave (SAM BSJ/4B1); 2A, 2B: M_3 (MW) of *H. equinus* from Nelson Bay Cave (SAM BSJ/94G7); 3A, 3B: M_3 (EW) of *H. leucophaeus* from Nelson Bay Cave (SAM CS/3B5); 4A, 4B: dP_2 (EW), dP_3 (MW), dP_4 (MW), M_1 (EW), M_2 (unerupted) of *H. leucophaeus* from Lake Pleasant (SAM Q1777). (Drawings by K. Scott.)

Table 2

Geographic origin of the comparative specimens of *Hippotragus* used in this study.

	NUMBER OF SPECIMENS		
	<i>H. equinus</i>	<i>H. niger</i> subsp.	<i>H. niger varians</i>
South Africa (Transvaal)	5	22	0
Swaziland	1	0	0
South West Africa	1	0	0
Botswana	1	2	0
Rhodesia	5	8	0
Zambia	45	31	0
Malawi	2	0	0
Angola	0	0	1
No provenance given in museum catalogues	39	19	0
TOTALS	99	82	1

DEFINITION OF THE MEASUREMENTS

The only dimension measured on both fossil and recent teeth was maximum length at the level of the occlusal surface, on the buccal side for maxillary teeth and on the lingual side for mandibular ones. Whenever possible (mainly on the comparative specimens), maximum length of whole premolar and molar rows were also recorded. The maximum length measurement has the dual advantage of analytic utility and easy definition and replication. Furthermore, it is the dental measurement most frequently used by other investigators of bovid fossils (see, for example, Gentry 1966 or 1970).

Casual observation is sufficient to show that the individual teeth, and especially the molars of *Hippotragus* spp., change length as they wear. In order to reduce sample variance and possible sample bias from this factor, four wear categories were defined and only measurements on homologous teeth in the same wear category are compared below, except in the case of whole molar and premolar rows where observation suggests there is relatively little length change with wear in any case (as some teeth grow shorter within a row, others become correspondingly longer). For the molars, the four wear categories are: (1) No Wear (NW)—no obvious wear on the molar crown; (2) Early Wear (EW)—wear on the crown obvious, but basal pillar not part of occlusal surface; (3) Medium Wear (MW)—basal pillar part of occlusal surface but tooth still characterized by considerable height above the alveolus (or on isolated teeth above the roots); and (4) Late Wear (LW)—tooth worn down to near the level of the alveolus (or, in the case of isolated teeth, to near the level of the roots, with occlusal surface very flat and smooth). The same four categories were used for the premolars (both deciduous and permanent), but are harder to define because, with the exception of dP₄, the premolars do not generally possess basal pillars. Separation of premolars in Early Wear and in Medium Wear is thus particularly difficult, but tests made to see whether the same tooth would be classified in the



Fig. 2. *Hippotragus leucophaeus*. Horn core from Nelson Bay Cave (SAM YGL 53/G3).

same wear category in successive weeks included no failures, suggesting that, however difficult to define, wear category judgements were at least consistent. In any case, the premolars do not change shape and length from Early Wear to Medium Wear as dramatically as the molars do so that confusion of premolar wear categories is unlikely to seriously affect any conclusions reached below.

Since most of the fossil horn cores lack the tip and sometimes a good part of the length adjacent to the tip, and since the sheaths could not be completely removed from many of the comparative specimens, horn-core measurements were restricted to the maximum longitudinal (antero-posterior) and transverse (medio-lateral) diameters immediately above the pedicel. These diameters are useful not only in themselves, but also because the ratio between them is a measure of transverse (side-to-side) compression. Thus, taken together, they may be used to say something about both the size and the shape of a basal horn-core cross-section. One difficulty in using the diameters to compare hippotragine species, however, is the fact that there are very great differences in basal horn-core size and shape between subadults and adults and between males and females within both *H. equinus* and *H. niger*. (In both species, young females have the smallest, most rounded horn-core bases, adult males the largest, most transversely compressed ones.) Sex is easy enough to take into account, but age is somewhat more difficult (for the teeth it is implicitly taken into account by the use of the wear categories). Since the bony consistency (solidity and non-porosity) of all the fossil horn cores suggested they belonged to adults or near-adults, I decided to concentrate on measurements of obviously adult specimens in the comparative collections. Because I could not always determine adulthood by examination of the cores themselves (frequently I could not remove the sheaths sufficiently), I relied on a dental state (upper and lower M3's both in at least Early Wear) as a rough index.

Appendix 1 presents the basic statistical parameters (\bar{x} = arithmetic mean, N = sample size, s = standard deviation) for each dental and horn-core category within *H. equinus*, *H. niger*, and each of the fossil samples. For *H. equinus* and *H. niger* the data are further broken down by sex, including a category in which known males, known females, and specimens of unknown sex are lumped. For *H. equinus*, *H. niger*, and those (few) fossil specimens for which matching left and right halves were available, only measurements on the left half were used to calculate the parameters in Appendix 1. All measurements were made in millimetres with the same dial-reading Helios calipers.

ANALYSIS OF THE MEASUREMENTS

Although a variety of statistical procedures, including multi-variate ones, could be used to analyse the numbers in Appendix 1, it was felt that the easily understood 't test' for statistically significant differences between two means, together with an intuitive appreciation for the size and patterning of differences, would be adequate to deal with the questions that prompted the analysis. Values

of 't' between paired means were calculated using a modified version of Programme BMDX70 on the CDC 6400 at the University of Washington computer centre (the same programme also calculated the means, standard deviations, and coefficients of variation found in Appendix 1). Those samples whose means were found to differ from one another at the 0.05 significance level or below are listed in Appendix 2. The sample with the larger mean is always to the left. In each case, the value of 't', the number of degrees of freedom (df), and the actual significance level of the differences (p) are given in succeeding columns.

Appendix 2, in conjunction with Appendix 1, can be used to support the following propositions:

(1) There is very little evidence for sexual dimorphism in tooth length in either *H. equinus* or *H. niger*. Such sex differences as may exist are small and there is reasonable justification for lumping measurements from both sexes in comparing *H. equinus* and *H. niger* with each other and with the fossil samples, which cannot be partitioned according to sex in any case. It is also relevant to point out that the coefficients of variation ($100s/\bar{x}$) (Appendix 1) are not substantially different for the mixed sex samples of teeth than for the single sex ones, suggesting again that lumping the sexes for comparison with the fossil samples is reasonable.

(2) The various teeth of *H. equinus* are longer than their counterparts in *H. niger*, the differences being especially great for the premolars. The premolars of *H. niger variati* are not significantly different in size from those of the remainder of the *H. niger* sample, but the molars are significantly longer, approaching those of *H. equinus* in length.

(3) The dental samples from Elands Bay, Elandsfontein, Bloembos, Swartklip, Eyre's Cave, Hawston, Lake Pleasant, and Klasies River Mouth are all very similar in mean measurements for any given category. Relatively few statistically significant differences can be demonstrated among these samples, and those that do exist tend to be small. Teeth in each of the cited samples are consistently shorter than corresponding teeth in *H. equinus*, the differences being especially marked for the molars. The premolars in the various samples tend to be significantly longer than those of *H. niger*, while the molars are roughly comparable in length to those of *H. niger*, though small differences in mean molar length between these samples and *H. niger* can be demonstrated statistically in some cases.

(4) Significant differences between the means of dental samples from Nelson Bay Cave, Oakhurst, and Uniondale on the one hand and those of the various fossil samples considered under (3) on the other are fairly common, with Nelson Bay, Oakhurst, and Uniondale means larger than the others in every case. Additionally, the means of the Nelson Bay, Oakhurst, and Uniondale dental samples differ from those discussed in (3) in being sometimes significantly larger and sometimes significantly smaller than those of *H. equinus*. At the same time, the means for both the molars and the premolars in the Nelson Bay, Oakhurst, and Uniondale samples tend to be significantly larger than those of *H. niger*.

Clearly there is justification for lumping Nelson Bay, Oakhurst, and Uniondale together as a group distinct from the other fossil samples. The peculiar behaviour of the Nelson Bay, Oakhurst, and Uniondale samples with respect of *H. equinus* strongly suggests that they are mixed, that is, that each contains material from more than one species, while the extent and nature of the mixture varies from dental category to dental category within each sample. Species mixture is particularly indicated for the Nelson Bay sample in which several dental categories exhibit relatively high coefficients of variation (Appendix 1), especially considering the comparatively small sample sizes.

The small dental samples from Melkhoutboom and Cradock Springs behave similarly to those from Nelson Bay, Oakhurst, and Uniondale with respect to the other samples, both fossil and comparative, except there is no instance in which a Melkhoutboom or Cradock Springs mean is significantly less than one for *H. equinus*.

(5) The *Hippotragus* skull in Glasgow that Broom assigned to *H. leucophaeus* is difficult to compare with the fossil samples because the only measurements available on it are maximum lengths of the entire premolar and molar rows. Intact molar and premolar rows are very poorly represented in the fossil samples. Additionally, alone among the measurements presented here, those on the Glasgow specimen were not made by the author, but were extracted from Mohr (1967: 62). Using these measurements, the Glasgow specimen is distinguishable from *H. equinus* by its significantly smaller upper and lower premolar rows and from *H. niger* by its significantly smaller upper premolar row. If the Glasgow skull derives from *H. leucophaeus*, this difference from *H. niger* is difficult to understand (a longer premolar row than in *H. niger* would be expected—see conclusions below based on proposition 3 above), and it is possible that a misprint in Mohr is responsible. (If the upper premolar row were 45,50 mm instead of 35,50 mm as given by Mohr, the Glasgow specimen would be indistinguishable from *H. niger* in upper premolar row length.) It must be concluded that the present study has not clarified the specific identity of the Glasgow skull, though on the basis of characters which are not considered here, but which may be seen in Mohr's photographs, I think it is highly likely the Glasgow specimen belongs to *H. niger*. This conclusion has been reached independently by Gentry (pers. comm.).

(6) Although the fossil horn cores cannot be 'sexed' to make them strictly comparable to those of *H. equinus* and *H. niger*, in both of which there is significant and substantial horn-core dimorphism, it is interesting that the average transverse diameter of the fossil specimens is closely comparable to that of both *H. equinus* and *H. niger* females, while their average longitudinal diameter significantly exceeds that of the females of either species. This suggests that the fossil males and females possessed smaller horn-core bases than the corresponding sexes in either *H. equinus* or *H. niger*, while the degree of transverse compression characterizing each sex in the fossil group was more comparable to that found in the sexes of *H. niger* than in those of *H. equinus*.

CONCLUSIONS

It seems reasonable to conclude that the relatively homogeneous material from Elands Bay, Elandsfontein, Bloembos, Swartklip, Eyre's Cave, Hawston, Lake Pleasant, and Klasies River Mouth derives from a single species of *Hippotragus* which may be differentiated from *H. equinus* by substantially smaller molars and premolars, and by smaller, more transversely compressed horn cores. It may be differentiated from *H. niger* by its larger premolars, higher premolar row to molar row length ratio and smaller horn cores. Since the various sites lie in or near the area where *H. leucophaeus* was encountered historically, and since there is nothing in the contrasts with *H. equinus* and *H. niger* that is contradicted by historical accounts of *H. leucophaeus*, it is only logical to assume that the species represented at the fossil sites is *Hippotragus leucophaeus*. The fact that a few small, but significant differences exist among the presumed *H. leucophaeus* samples is not surprising, considering their spread over a span of tens of thousands of years.

The most economical explanation of the relatively heterogeneous material from Oakhurst, Nelson Bay Cave, and Uniondale is that it results from a mixture of *H. leucophaeus* and a closely related, but significantly larger species. The most reasonable candidate for the second species is *H. equinus*, though if this is accepted, the data in Appendices 1 and 2 imply that the now extinct southern Cape *H. equinus* was significantly larger than the recent central African variety that dominates the comparative sample. The probable distributional overlap of *H. leucophaeus* and *H. equinus* at Uniondale, Oakhurst, and especially at Nelson Bay, where overlap seems to have lasted for several millennia, clearly suggests that the two forms are separate species and not simply subspecies. As indicated by Mohr (1967: 20-21), many nineteenth-century authors and some twentieth-century ones have regarded *H. leucophaeus* as only a subspecies of *H. equinus*. Interestingly, overlap in the vicinity of Nelson Bay Cave may have continued into historic times if, as Mohr (1967: 16) reasonably suggests, an animal seen and illustrated in 1778 by Gordon near Plettenberg Bay was a roan and not a blue antelope.

The small samples from Melkhoutboom and Cradock Springs are most reasonably assigned to *H. equinus*. Whether or not *H. leucophaeus* was also represented in the vicinity of these sites must remain uncertain until larger samples are collected.

The fossil data suggest that *H. leucophaeus* was both more widely distributed and more numerous in the past than at time of historic contact. In the earlier part of the Last Glacial, it occurred both east of Plettenberg Bay (at Klasies River Mouth) and west of the Hottentots Holland Mountains (at Swartklip and perhaps also at Elandsfontein).² During this time interval (roughly between 70 000 and 35 000 B.P.), *H. leucophaeus* may have been the only

² It is the geological antiquity and not the specific assignment of the material from Elandsfontein that is problematical.

species of *Hippotragus* in the southern Cape (at least south of the mountains of the Cape Folded Belt). Both well-dated, earlier Last Glacial sites have provided fairly large *Hippotragus* samples with no hint of species mixture. At both sites, the frequency of *H. leucophaeus* vs. that of other taxa in the fossil assemblages is relatively high, suggesting that *H. leucophaeus* was a fairly common antelope.

H. leucophaeus may have maintained its broader-than-historic distribution throughout the Last Glacial, though this cannot be established at present. It can be said, however, that it was fairly numerous near Nelson Bay Cave near the end of the Last Glacial, while in the early Holocene, it once again occurred far outside its historic limits, as far west as Elands Bay and as far east as Uniondale Shelter.

The time when the ranges of *H. equinus* and *H. leucophaeus* first overlapped remains uncertain, but some clues may be obtained by examination of dental samples from the different levels of Nelson Bay Cave. Although there is no statistical technique which will separate mixed Nelson Bay samples into discrete *H. equinus* and *H. leucophaeus* subsamples, it is possible to use an arbitrary cut-off point to determine if the extent of mixture seems to have changed through time. Molars are more useful than premolars in this context since they contrast more in mean size between *H. equinus* and *H. leucophaeus* (as found unmixed at Swartklip, Klasies River Mouth, etc.) than do premolars. Limited experimentation with the data in Appendix 1 showed that a useful arbitrary cut-off point was the mean length for each wear category of each *H. equinus* molar minus the standard deviation for that category. In Table 3, the number of molars smaller than this arbitrary standard in each of the major culture-stratigraphic units of Nelson Bay is presented in the left-hand column, the number of molars larger than the standard appears on the right. For the sake of comparison, the apparently homogeneous sample from Klasies River Mouth, considerably older than any of the Nelson Bay samples, has been partitioned in the same manner and included in the bottommost row of Table 3.

Table 3 clearly shows that the 11 000–8 000 year unit at Nelson Bay (Albany culture-stratigraphic unit) is characterized by a significantly larger number of teeth, longer than the arbitrary standard than are the other two Nelson Bay units or the Klasies unit. These data may be used to argue strongly that *H. equinus* only became prominent at Nelson Bay after 11 000 B.P. or even that it only first appeared there at that time. More sophisticated techniques applied to larger samples than are presently available may allow a more conclusive statement at some future date.

11 000 B.P. was a time when not only culture but also environment was changing at Nelson Bay Cave. Evidence from analysis of the entire fauna (Klein 1972b) indicates that extensive stretches of grassland present prior to 11 000 B.P. were shrinking, probably as a consequence of bush-forest encroachment, perhaps in combination with drowning of much of the coastal plain by the terminal Last Glacial rise in sea-level. It is entirely possible that this environmental change was what brought *H. equinus* into the area, or if it was already there, led

Table 3

Comparison of the frequencies of *Hippotragus* molars above and below an arbitrary standard length in the different culture-stratigraphic units of Nelson Bay and Klasies River Mouth caves.

Culture-stratigraphic units	Number of molars smaller than the <i>H. equinus</i> mean minus one standard deviation from the <i>H. equinus</i> mean	Number of molars larger than the <i>H. equinus</i> mean minus one standard deviation from the <i>H. equinus</i> mean	Approx. C-14 years B.P.
			5 000
Wilton (Nelson Bay)	5 (56%) A	4 (44%) B	
			8 000
Albany (Nelson Bay)	11 (20%) C	43 (80%) D	
			11 000
Robberg (Nelson Bay)	26 (74%) E	9 (26%) F	
			18 500
MAJOR TIME BREAK			
			≥ 30 000
Middle Stone Age (Klasies River Mouth)	105 (76%) G	34 (24%) H	
			780 000

Chi-square values

$$\frac{AB}{CD} = 5,027, p = 0,05-0,02$$

$$\frac{CD}{EF} = 25,413, p < 0,001$$

$$\frac{EF}{GH} = 0,024, p = 0,90-0,80$$

to its increase relative to *H. leucophaeus*, as suggested by Table 3. If so, we have evidence for a possible ecological contrast between *H. leucophaeus* and *H. equinus*—though both were probably mainly grazers, *H. leucophaeus* could be inferred to have preferred somewhat more open habitats than *H. equinus*. The same sort of contrast has been observed between *H. niger* and *H. equinus* (in this case it is *H. equinus* that seems to prefer the slightly more open situations—Child and Wilson 1964), though very little else is known about their ecological differences. It is interesting that the frequency of *H. leucophaeus* vs. *H. equinus* at Nelson Bay may have shifted again after c. 8 000 B.P. (as indicated by Table 3), since there is independent evidence for further environmental change around Nelson Bay at that time. Unfortunately, its precise nature remains undetermined (Klein 1972a).

At the time of historic contact, it seems probable that *H. leucophaeus* was already very much reduced in range and numbers from prior times and that Europeans and European weapons only delivered the *coup de grâce*. It is unclear what may have led to its decline prior to the arrival of Europeans, but the principal factor may have been habitat deterioration, following the introduction of domestic sheep. These have now been documented as early as A.D. 400 for the south-western Cape (Schweitzer & Scott 1973). Interestingly, *H. equinus* is presently in a state of decline which is not clearly linked to human predation (Ansell 1971: 46), but which may in fact relate in complex fashion to the introduction of domestic stock over much of its range. Future research at archaeological and palaeontological sites in the southern Cape should provide data to help explain the decline of *H. leucophaeus* as well as more information on its appearance, habitat preferences, and past distribution.

SUMMARY

The blue antelope, *Hippotragus leucophaeus*, was encountered by early European travellers to the Cape in a small area centring on the triangle Swellendam–Caledon–Bredasdorp. It was apparently never numerous in historic times and became extinct around A.D. 1800, before qualified scientists could make observations on live specimens. This paper analyses relevant fossil material from several Upper Pleistocene and Holocene localities in the southern Cape in an attempt to resolve some outstanding questions on the taxonomic status, distribution, and ecology of *H. leucophaeus*. It is concluded that it was a good species (not simply a subspecies of the roan, *H. equinus*), that at various times in the past it was both more numerous and more widely distributed than at time of historic contact, and that it probably preferred somewhat more open habitats than its close relative, *H. equinus*, with which it apparently overlapped throughout much of the Holocene, at least in the vicinity of Plettenberg Bay.

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Appendix 1

Arithmetic mean (\bar{x}), sample size (N), standard deviation (s), and coefficient of variation ($V = 100s/\bar{x}$) for each tooth length and horn-core diameter in the various *Hippotragus* samples considered in the text. NW = No Wear, EW = Early Wear, MW = Medium Wear, LW = Late Wear (for definition of the wear categories, see the text). MM, FF, ?? = Males, Females, and specimens of unknown sex.

dP₂—dP₄

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>Swartklip</i>	<i>Klasies</i>	<i>Lake Pleasant</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??			
\bar{x}	56,57	59,13	57,41	49,06	49,35	49,60	55,50	54,00	51,00
N	13	7	30	7	4	12	5	3	1
s	2,740	4,357	3,827	2,180	1,601	2,385	2,791	4,498	—
V	4,8	7,4	6,6	4,4	3,2	4,8	5,0	8,3	—

dP²—dP⁴

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>Swartklip</i>	<i>Klasies</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??		
\bar{x}	58,11	60,26	58,88	52,72	53,40	53,38	58,40	54,00
N	15	12	40	6	5	12	1	2
s	2,819	2,946	3,092	1,347	3,083	2,418	—	2,121
V	4,9	4,9	5,3	2,6	5,8	4,5	—	3,9

P₂—P₄

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger varianti</i>			<i>Swartklip</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??	
\bar{x}	51,51	50,05	51,02	44,32	44,00	44,09	45,50	—	—	49,30
N	9	11	31	23	25	52	1	—	—	3
s	1,593	3,005	2,330	3,081	2,025	2,515	—	—	—	3,534
V	3,1	6,1	4,6	7,0	4,6	5,7	—	—	—	7,1
	<i>Klasies</i>	<i>Nelson Bay</i>	<i>Hawston</i>	<i>Bloembos</i>	<i>Glasgow</i>					
\bar{x}	43,90	53,40	46,70	50,40	45,50					
N	1	1	1	1	1					
s	—	—	—	—	—					
V	—	—	—	—	—					

M ₁ —M ₃			<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Swartklip</i>				
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??							
\bar{x}	77,71	77,74	77,55	71,43	70,04	70,60	76,40	—	—				71,15			
N	15	14	45	28	30	63	1	—	—				4			
s	3,191	2,766	2,749	3,528	3,332	3,440	—	—	—				1,168			
V	4,1	3,6	3,5	4,9	4,8	4,9	—	—	—				1,6			
<i>Nelson Bay</i>			<i>Elandsfontein</i>			<i>Eyre's Cave</i>			<i>Bloembos</i>			<i>Glasgow</i>				
\bar{x}	74,30		70,30	65,80	72,55	72,00										
N	1		3	1	1	1										
s	—		1,623	—	—	—										
V	—		2,6	—	—	—										
P ₂ —P ₄ /M ₁ —M ₃			<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Swartklip</i>			<i>Bloembos</i>	<i>Glasgow</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??							
\bar{x}	0,661	0,640	0,656	0,620	0,629	0,624	0,596	—	—				0,694	0,695	0,632	
N	9	11	31	22	25	51	1	—	—				3	1	1	
s	0,030	0,052	0,038	0,040	0,020	0,030	—	—	—				0,051	—	—	
V	4,5	8,2	5,8	6,5	3,1	4,8	—	—	—				7,4	—	—	
P ² —P ⁴			<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Swartklip</i>				
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??							
\bar{x}	52,74	52,50	52,63	46,50	45,61	45,86	46,35	—	—				50,10			
N	11	22	55	24	25	56	1	—	—				1			
s	1,575	2,732	2,656	2,734	2,432	2,509	—	—	—				—			
V	3,0	5,2	5,0	5,5	5,3	5,5	—	—	—				—			
<i>Klasies</i>			<i>Eyre's Cave</i>			<i>Glasgow</i>										
\bar{x}	49,73	49,30	35,50													
N	3	1	1													
s	2,230	—	—													
V	4,5	—	—													

M¹—M³

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Swartklip</i>	<i>Klasies</i>	<i>Nelson Bay</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??			
\bar{x}	72,52	70,35	70,77	66,63	64,64	65,58	71,60	—	—	67,37	63,10	69,00
N	15	23	66	31	30	68	1	—	—	3	2	1
s	3,316	2,670	2,985	3,454	3,475	3,450	—	—	—	3,157	—	—
V	4,6	3,8	4,2	5,2	5,4	5,3	—	—	—	4,7	—	—
	<i>Elandsfontein</i>		<i>Glasgow</i>									
\bar{x}	69,50		66,50									
N	1		1									
s	—		—									
V	—		—									

P²—P⁴/M¹—M³

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Swartklip</i>	<i>Klasies</i>	<i>Glasgow</i>
	Males	Females	MM,FF,??	Males	Females	MM,FF,??	Males	Females	MM,FF,??			
\bar{x}	0,740	0,745	0,748	0,697	0,708	0,700	0,647	—	—	0,761	0,808	0,549
N	10	22	54	24	24	54	1	—	—	1	2	1
s	0,044	0,034	0,035	0,030	0,029	0,030	—	—	—	—	0,009	—
V	5,9	4,6	4,7	4,3	4,1	4,2	—	—	—	—	1,1	—

Horn-core base—Medio-lateral (transverse) diameter

	<i>H. equinus</i>			<i>H. niger</i> subsp.			<i>H. niger variati</i>			<i>Klasies</i>
	Male	Female	MM,FF,	Male	Female	MM,FF,	Male	Female	MM,FF,	
	adults	adults	all ages	adults	adults	all ages	adults	adults	all ages	
\bar{x}	49,05	38,35	42,93	49,42	39,64	43,41	60,15	—	—	40,82
N	4	6	35	11	17	37	1	—	—	5
s	5,608	3,038	6,631	5,150	3,854	6,985	—	—	—	3,962
V	11,4	7,9	14,8	10,4	9,7	16,1	—	—	—	9,7
	<i>Nelson Bay</i>		<i>Elandsfontein</i>	<i>Sum of three previous</i>						
\bar{x}	42,60		43,14	42,21						
N	1		7	13						
s	—		3,405	3,537						
V	—		8,0	8,4						

Swartklip				Klasies				Nelson Bay			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 17,27	—	16,20	—	17,44	19,15	—	16,53	18,50	18,20	17,90	17,95
N 6	—	2	—	8	2	—	4	7	3	3	2
S 0,943	—	0,566	—	0,573	0,919	—	0,427	0,872	0,954	0,854	0,495
V 5,5	—	3,5	—	3,3	4,8	—	2,6	4,7	5,2	4,8	2,8

Lake Pleasant			
NW	EW	MW	LW
\bar{x} —	—	17,00	—
N —	—	1	—
S —	—	—	—
V —	—	—	—

dP₄

<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} —	—	27,10	24,57	—	31,00	28,28	26,33	29,30	31,00	27,73	25,15
N —	—	3	12	—	1	4	3	1	1	10	21
S —	—	1,825	1,244	—	—	2,090	0,551	—	—	1,926	1,529
V —	—	6,7	5,1	—	—	7,4	2,1	—	—	6,9	6,1

<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM,FF,??			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} —	—	24,50	22,78	—	—	24,65	23,10	—	—	24,95	22,86
N —	—	1	6	—	—	2	2	—	—	4	8
S —	—	—	1,339	—	—	—	1,556	—	—	0,704	1,284
V —	—	—	5,9	—	—	—	6,7	—	—	2,8	5,6

Swartklip				Klasies				Nelson Bay			
NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x} 27,57	28,70	26,50	—	27,95	27,64	29,60	23,18	28,28	31,70	29,05	24,05
N 6	1	2	—	6	5	1	4	5	1	2	4
S 1,518	—	2,121	—	0,703	1,610	—	0,903	1,130	—	0,778	1,134
V 5,5	—	8,0	—	2,5	5,8	—	3,9	4,0	—	2,7	4,6

[illegible]

				<i>Nelson Bay</i>			
				EW	MW	NW	LW
\bar{x}	—	—	—	—	—	22,67	—
N	—	—	—	—	—	3	—
s	—	—	—	—	—	1,501	—
V	—	—	—	—	—	6,6	—
				<i>Klasies</i>			
				EW	MW	LW	LW
\bar{x}	—	—	—	19,95	18,50	—	—
N	—	—	—	2	1	—	—
s	—	—	—	0,212	—	—	—
V	—	—	—	1,1	—	—	—
				<i>Uniondale</i>			
				EW	MW	LW	LW
\bar{x}	—	—	—	—	—	17,70	—
N	—	—	—	—	—	1	—
s	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—
				<i>Eyre's Cave</i>			
				EW	MW	LW	LW
\bar{x}	20,00	—	—	—	—	—	—
N	1	—	—	—	—	—	—
s	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—
P_2				<i>H. equinus</i> —Males			
				EW	MW	LW	LW
\bar{x}	13,40	14,28	13,90	—	—	—	—
N	2	6	1	—	—	—	—
s	—	0,988	—	—	—	—	—
V	—	6,8	—	—	—	7,2	—
				<i>H. equinus</i> —Females			
				EW	MW	LW	LW
\bar{x}	12,65	12,80	10,80	—	—	—	—
N	4	4	1	—	—	—	—
s	0,914	0,497	—	—	—	—	—
V	3,9	—	—	—	—	—	—
				<i>H. equinus</i> —MM,FF,??			
				EW	MW	NW	LW
\bar{x}	13,04	13,60	13,35	—	—	—	—
N	8	16	6	—	—	—	—
s	0,953	1,039	1,624	—	—	—	—
V	7,3	7,6	12,2	—	—	—	—
				<i>H. niger</i> subsp.—Males			
				EW	MW	LW	LW
\bar{x}	11,77	11,37	—	—	—	—	—
N	13	3	—	—	—	—	—
s	1,387	1,050	—	—	—	—	—
V	11,8	9,2	—	—	—	—	—
				<i>H. niger</i> subsp.—Females			
				EW	MW	LW	LW
\bar{x}	12,18	12,15	11,90	—	—	—	—
N	5	15	4	—	—	—	—
s	0,646	1,006	0,627	—	—	—	—
V	5,3	8,3	5,3	—	—	—	—
				<i>H. niger</i> subsp.—MM,FF,??			
				EW	MW	NW	LW
\bar{x}	11,96	11,67	10,10	—	—	—	—
N	32	7	1	—	—	—	—
s	1,125	0,804	—	—	—	—	—
V	9,4	6,9	—	—	—	—	—
				<i>H. niger varians</i> —Males			
				EW	MW	LW	LW
\bar{x}	12,60	—	—	—	—	—	—
N	1	—	—	—	—	—	—
s	—	—	—	—	—	—	—
V	—	—	—	—	—	—	—
				<i>Swartklip</i>			
				EW	MW	LW	LW
\bar{x}	12,75	—	—	—	—	—	—
N	4	—	—	—	—	—	—
s	1,529	—	—	—	—	—	—
V	12,0	—	—	—	—	—	—
				<i>Klasies</i>			
				EW	MW	NW	LW
\bar{x}	11,80	13,48	14,20	—	—	—	—
N	3	5	1	—	—	—	—
s	0,458	1,472	—	—	—	—	—
V	3,9	10,9	—	—	—	—	—

Nelson Bay					Bloembos				Hawston			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	13,33	13,28	—	13,00	—	13,15	—	—	—	—	13,10	—
N	6	10	—	1	—	1	—	—	—	—	1	—
s	0,905	1,589	—	—	—	—	—	—	—	—	—	—
V	6,8	12,0	—	—	—	—	—	—	—	—	—	—
Oakhurst												
	NW	EW	MW	LW								
\bar{x}	12,65	—	—	—								
N	2	—	—	—								
s	12,02	—	—	—								
V	9,5	—	—	—								
P ₃	<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	15,30	18,15	17,37	18,70	—	18,30	16,80	16,77	15,30	18,46	17,47	17,25
N	1	8	3	1	—	10	1	3	1	25	7	6
s	—	0,832	1,097	—	—	0,793	—	0,702	—	0,924	0,883	0,871
V	—	4,6	6,3	—	—	4,3	—	4,1	—	5,0	5,1	5,1
	<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM,FF,??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	15,84	15,57	14,00	14,50	15,89	15,22	14,60	14,50	15,80	15,82	14,40
N	—	14	9	2	1	16	6	4	1	32	18	6
s	—	1,136	1,084	0,707	—	0,804	1,080	1,257	—	0,943	2,470	1,070
V	—	5,7	7,0	5,1	—	5,3	7,1	8,6	—	5,9	15,6	7,4
	<i>H. niger varianti</i> —Males				Swartklip				Klasies			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	17,05	—	—	—	16,98	17,30	—	17,20	16,73	16,76	16,00
N	—	1	—	—	—	4	1	—	3	4	5	2
s	—	—	—	—	—	0,613	—	—	1,179	0,727	0,716	1,131
V	—	—	—	—	—	3,6	—	—	6,9	4,3	4,3	7,1

	x	N	s	V		x	N	s	V		x	N	s	V	P ₄		x	N	s	V		x	N	s	V
<i>Nelson Bay</i>	NW	—	—	—	—	NW	—	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	—	—	—
	EW	17,50	1,445	8,3	—	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,38	6	6,8	—	EW	15,78	13	5,6
	MW	18,23	0,709	3,9	—	MW	15,55	—	—	—	MW	—	—	—	—	—	MW	17,97	3	3,1	—	MW	15,61	8	6,8
	LW	19,70	4	—	—	LW	1	—	—	—	LW	17,60	—	—	—	—	LW	19,50	1	—	—	LW	14,70	1	—
			1	—	—				—	—				—	—	—				—				—	—
<i>Elandsfontein</i>	NW	—	—	—	—	NW	16,60	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	15,40	1	—
	EW	17,20	—	—	—	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,80	9	0,487	2,6	EW	16,00	16	6,9
	MW	17,15	0,636	3,7	—	MW	—	—	—	—	MW	—	—	—	—	—	MW	18,70	1	—	—	MW	16,14	5	4,9
	LW	—	—	—	—	LW	—	—	—	—	LW	—	—	—	—	—	LW	18,18	4	0,896	4,9	LW	15,58	5	6,6
<i>Bloembos</i>	NW	—	—	—	—	NW	—	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	15,30	3	3,3
	EW	—	—	—	—	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,51	25	0,932	5,0	EW	15,94	31	6,2
	MW	17,60	—	—	—	MW	—	—	—	—	MW	—	—	—	—	—	MW	18,34	5	0,658	3,6	MW	15,74	16	5,8
	LW	—	—	—	—	LW	18,40	—	—	—	LW	—	—	—	—	—	LW	18,74	9	0,934	5,0	LW	15,38	8	7,2
			1	—	—				—	—				—	—	—				—				—	—
<i>Uitendale</i>	NW	—	—	—	—	NW	—	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	—	—	—
	EW	—	—	—	—	EW	—	—	—	—	EW	—	—	—	—	—	EW	—	—	—	—	EW	—	—	—
	MW	—	—	—	—	MW	—	—	—	—	MW	—	—	—	—	—	MW	—	—	—	—	MW	—	—	—
	LW	—	—	—	—	LW	—	—	—	—	LW	—	—	—	—	—	LW	—	—	—	—	LW	—	—	—
<i>H. niger</i> subsp. —Males	NW	15,05	2	0,354	2,3	NW	—	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	—	—	—
	EW	15,78	13	0,878	5,6	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,38	6	6,8	—	EW	15,78	13	5,6
	MW	15,61	8	1,067	6,8	MW	—	—	—	—	MW	—	—	—	—	—	MW	17,97	3	3,1	—	MW	15,61	8	6,8
	LW	14,70	1	—	—	LW	—	—	—	—	LW	—	—	—	—	—	LW	19,50	1	—	—	LW	14,70	1	—
<i>H. niger</i> subsp. —Females	NW	15,40	1	—	—	NW	16,60	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	15,40	1	—
	EW	16,00	16	1,099	6,9	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,80	9	0,487	2,6	EW	16,00	16	6,9
	MW	16,14	5	0,789	4,9	MW	—	—	—	—	MW	—	—	—	—	—	MW	18,70	1	—	—	MW	16,14	5	4,9
	LW	15,58	5	1,027	6,6	LW	—	—	—	—	LW	—	—	—	—	—	LW	18,18	4	0,896	4,9	LW	15,58	5	6,6
<i>H. niger</i> subsp. —MM, FF, ??	NW	15,30	3	0,500	3,3	NW	—	—	—	—	NW	—	—	—	—	—	NW	—	—	—	—	NW	15,30	3	3,3
	EW	15,94	31	0,981	6,2	EW	—	—	—	—	EW	—	—	—	—	—	EW	18,51	25	0,932	5,0	EW	15,94	31	6,2
	MW	15,74	16	0,915	5,8	MW	—	—	—	—	MW	—	—	—	—	—	MW	18,34	5	0,658	3,6	MW	15,74	16	5,8
	LW	15,38	8	1,102	7,2	LW	—	—	—	—	LW	—	—	—	—	—	LW	18,74	9	0,934	5,0	LW	15,38	8	7,2

	<i>H. niger variati</i> —Males					<i>Swartklip</i>					<i>Klasies</i>			
	NW	EW	MW	LW		NW	EW	MW	LW		NW	EW	MW	LW
\bar{x}	—	—	—	19,95		25,40	23,40	20,10	—		22,92	21,83	20,38	18,75
N	—	—	—	1		1	1	6	—		9	4	13	8
s	—	—	—	—		—	—	0,777	—		0,692	1,343	1,190	1,255
V	—	—	—	—		—	—	3,9	—		3,0	6,2	5,8	6,7
	<i>Nelson Bay</i>					<i>Elandsfontein</i>					<i>Bloembos</i>			
	NW	EW	MW	LW		NW	EW	MW	LW		NW	EW	MW	LW
\bar{x}	22,75	25,33	21,40	20,70		—	22,65	20,70	17,80		—	—	—	19,80
N	2	6	13	3		—	2	5	4		—	—	—	1
s	0,778	1,623	1,496	3,727		—	0,212	0,660	1,175		—	—	—	—
V	3,4	6,4	6,9	18,0		—	0,9	3,2	6,6		—	—	—	—
	<i>Oakhurst</i>					<i>Uniondale</i>					<i>Hawston</i>			
	NW	EW	MW	LW		NW	EW	MW	LW		NW	EW	MW	LW
\bar{x}	—	—	—	20,30		24,90	—	—	—		—	—	—	16,20
N	—	—	—	1		1	—	—	—		—	—	—	1
s	—	—	—	—		—	—	—	—		—	—	—	—
V	—	—	—	—		—	—	—	—		—	—	—	—
	<i>Eyre's Cave</i>					<i>Lake Pleasant</i>								
	NW	EW	MW	LW		NW	EW	MW	LW					
\bar{x}	—	—	16,60	16,20		—	23,10	—	—					
N	—	—	1	1		—	1	—	—					
s	—	—	—	—		—	—	—	—					
V	—	—	—	—		—	—	—	—					
M ₂	<i>H. equinus</i> —Males					<i>H. equinus</i> —Females					<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	LW		NW	EW	MW	LW		NW	EW	MW	LW
\bar{x}	26,62	26,26	24,85	22,80		25,63	26,30	24,62	23,87		26,16	26,18	24,64	23,72
N	5	7	10	1		3	2	11	3		12	12	34	6
s	0,719	1,263	1,161	—		0,907	1,272	1,072	0,651		0,812	1,021	1,076	0,674
V	2,7	4,8	4,7	—		3,5	4,8	4,4	2,7		3,1	3,9	4,4	2,8

M ₃	<i>H. equinus</i> —Males			<i>H. equinus</i> —Females			<i>H. equinus</i> —MM,FF,??		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	30,20	30,29	31,32	—	30,23	31,90	29,56	30,22	31,47
N	1	8	5	—	6	5	3	21	15
s	—	1,664	1,985	—	2,153	1,357	0,602	1,709	1,479
V	—	5,5	6,3	—	7,1	4,3	2,0	5,7	4,7
	<i>H. niger</i> subsp. — Males			<i>H. niger</i> subsp. — Females			<i>H. niger</i> subsp. — MM,FF,??		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	28,90	27,67	29,43	27,40	28,02	28,97	28,15	27,84	29,14
N	1	16	10	1	16	9	2	33	23
s	—	2,856	1,975	—	1,294	1,796	1,061	2,154	1,811
V	—	10,3	6,7	—	4,6	6,0	3,8	7,7	6,2
	<i>H. niger variati</i> —Males			<i>Swartklip</i>			<i>Klasies</i>		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	—	—	32,50	—	—	28,48	—	—	—
N	—	—	1	—	—	5	26,60	24,00	28,31
s	—	—	—	—	—	0,626	2	4	6
V	—	—	—	—	—	2,2	0,141	2,211	1,376
							0,5	9,2	4,7
	<i>Nelson Bay</i>			<i>Elandsfontein</i>			<i>Bloembos</i>		
	NW	EW	MW	NW	EW	MW	NW	EW	MW
\bar{x}	31,50	29,96	30,34	28,40	27,75	28,10	—	—	—
N	1	5	11	1	2	4	—	—	—
s	—	2,079	3,088	—	1,768	0,627	—	—	—
V	—	6,9	10,2	—	6,4	2,2	—	—	—
	<i>Eyre's Cave</i>								
	NW	EW	MW						
\bar{x}	—	—	27,90						
N	—	—	1						
s	—	—	—						
V	—	—	—						

P ²	<i>H. equinus</i> —Males				<i>H. equinus</i> —Females				<i>H. equinus</i> —MM, FF, ??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	16,47	17,70	17,60	—	16,87	17,38	17,82	—	16,94	17,12	17,94
N	—	7	3	1	—	13	4	4	—	32	13	10
S	—	1,188	0,500	—	—	0,998	1,670	1,597	—	1,004	1,141	1,852
V	—	7,2	2,8	—	—	5,9	9,6	9,0	—	7,0	6,7	10,3
	<i>H. niger</i> subsp.—Males				<i>H. niger</i> subsp.—Females				<i>H. niger</i> subsp.—MM, FF, ??			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	15,45	14,93	14,55	13,90	15,36	15,55	14,63	13,90	15,43	14,84	14,37
N	—	13	8	2	1	15	4	6	1	31	16	9
S	—	1,144	0,819	0,495	—	1,351	0,480	1,232	—	1,179	0,974	1,235
V	—	7,4	5,5	3,4	—	8,8	3,1	8,4	—	7,6	6,6	8,6
	<i>H. niger varianti</i> —Males				<i>Swartklip</i>				<i>Klasies</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	14,80	—	—	—	17,05	—	17,00	16,70	—	17,67
N	—	—	1	—	—	—	2	—	1	3	—	3
S	—	—	—	—	—	—	—	—	—	1,852	—	1,301
V	—	—	—	—	—	—	—	—	—	11,1	—	7,4
	<i>Nelson Bay</i>				<i>Elandsfontein</i>				<i>Hawston</i>			
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	17,19	18,30	16,13	—	16,30	—	16,90	—	—	—	16,10
N	—	8	3	3	—	1	—	1	—	—	—	1
S	—	1,410	1,114	0,802	—	—	—	—	—	—	—	—
V	—	8,2	6,1	5,0	—	—	—	—	—	—	—	—
	<i>Eyre's Cave</i>											
	NW	EW	MW	LW								
\bar{x}	—	—	—	18,20								
N	—	—	—	1								
S	—	—	—	—								
V	—	—	—	—								

P ⁴	<i>H. equinus</i> —Males			<i>H. equinus</i> —Females			<i>H. equinus</i> —MM,FF,??			
	NW	EW	MW	NW	EW	MW	NW	EW	MW	LW
\bar{x}	—	15,95	17,33	—	16,06	16,83	16,30	16,28	16,98	15,71
N	—	6	4	—	13	3	1	33	10	12
s	—	0,414	0,900	—	1,121	0,153	—	0,898	0,671	1,093
V	—	2,6	5,2	—	7,0	0,9	—	5,5	4,0	7,0

[illegible]

M ²	<i>H. equinus</i> —Males			<i>H. equinus</i> —Females			<i>H. equinus</i> —MM,FF,??					
	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	25,67	26,11	25,91	23,40	25,27	25,24	25,39	23,96	24,99	25,66	25,38	23,69
N	3	8	11	1	3	5	18	5	11	18	52	8
S	1,155	1,127	1,069	—	0,306	2,026	1,630	0,577	0,817	1,385	1,579	0,611
V	4,5	4,3	4,1	—	1,2	8,0	6,4	2,4	3,3	5,4	6,2	2,6
<i>H. niger</i> subsp.—Males												
<i>H. niger</i> subsp.—Females	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	24,73	23,72	—	—	24,33	23,07	21,30	—	24,61	23,31	21,30
N	—	9	24	—	—	4	22	5	—	13	55	5
S	—	0,782	1,489	—	—	1,646	1,508	1,017	—	1,060	1,501	1,017
V	—	3,1	6,3	—	—	6,8	6,5	4,8	—	4,3	6,4	4,8
<i>H. niger varians</i> —Males												
<i>H. niger</i> subsp.—Females	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	—	—	26,00	—	—	25,30	21,70	—	—	22,18	21,85	23,50
N	—	—	1	—	—	1	2	—	—	5	11	1
S	—	—	—	—	—	—	0,566	—	—	0,789	0,588	—
V	—	—	—	—	—	—	2,6	—	—	3,6	2,7	—
<i>Nelson Bay</i>												
<i>Elandsfontein</i>	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	24,50	22,83	—	24,50	22,55	22,85	23,00	—	—	24,90	—	24,60
N	2	7	—	1	2	2	1	—	—	1	—	1
S	2,828	1,285	—	—	0,353	0,919	—	—	—	—	—	—
V	11,5	5,6	—	—	1,6	4,0	—	—	—	—	—	—
<i>Cradock Springs</i>												
<i>Swartklip</i>	NW	EW	MW	LW	NW	EW	MW	LW	NW	EW	MW	LW
\bar{x}	28,00	27,10	—	—	22,55	22,85	23,00	—	—	24,90	—	24,60
N	1	1	—	—	2	2	1	—	—	1	—	1
S	—	—	—	—	0,353	0,919	—	—	—	—	—	—
V	—	—	—	—	1,6	4,0	—	—	—	—	—	—

Appendix 2

List of samples for which statistically significant mean differences exist, by category. t = value of 'Student's t', df = degrees of freedom, p = significance level. He = *H. equinus*, Hnv = *H. niger varians*, Hn = other *H. niger*, ZW = Swartklip, KRM = Klasies River Mouth, NBC = Nelson Bay Cave, EFT = Elandsfontein, BMB = Bloembos, HTN = Hawston, EC = Eyre's Cave, LP = Lake Pleasant, UND = Uniondale, OAK = Oakhurst, MHB = Melkhoutboom, CS = Cradock Springs, GGW = Glasgow, MM = Males, FF = Females.

	t	df	p		t	df	p
dP ₂ -dP ₄				P ₂ -P ₄			
He > Hn	6,55	40	< 0,001	M ₁ -M ₃			
ZW > Hn	4,43	15	< 0,001	ZW > Hn	3,83	52	< 0,001
KRM > Hn	2,42	13	0,031	BMB > Hn	3,32	51	0,002
dP ₂ -dP ₄				BMB > Hnv	13,46	2	0,005
He > KRM	2,19	40	0,034	P ₂ -P ₄			
He > Hn	5,66	50	< 0,001	He > Hn	13,82	109	< 0,001
P ₂ -P ₄				He > Hnv	3,31	55	0,002
He > Hn	12,48	81	< 0,001	He > GGW	6,39	54	< 0,001
He > Hnv	3,29	31	0,002	Hn > GGW	4,09	54	< 0,001
He > KRM	3,01	30	0,005	KRM > Hn	2,62	57	0,011
He > GGW	2,33	30	0,05-0,02	M ₁ -M ₃			
ZW > Hn	3,43	53	0,001	He > Hn	9,30	132	< 0,001
NBC > Hn	3,67	51	0,001	He > KRM	3,61	66	0,001
BMB > Hn	3,52	52	0,001	HnMM > HnFF	2,25	59	0,028
BMB > Hnv	3,43	53	0,021	Hnv > Hn	2,45	68	0,017
M ₁ -M ₃				P ₂ -P ₄			
He > Hn	11,22	106	< 0,001	M ₁ -M ₃			
He > ZW	4,58	47	< 0,001	He > Hn	7,69	106	< 0,001
He > EC	4,23	44	< 0,001	He > Hnv	4,02	54	< 0,001
He > EFT	4,49	46	< 0,001	He > GGW	5,63	53	< 0,001
He > BMB	2,54	45	0,014	Hn > GGW	4,99	53	< 0,001
Hnv > Hn	2,36	63	0,021	Hn > Hnv	2,48	54	0,015
Hnv > ZW	5,07	4	0,007	ZW > Hn	2,06	53	0,044
Hnv > EFT	4,35	3	0,022	KRM > He	2,42	54	0,019
ZW > EC	4,10	3	0,026	KRM > Hn	5,13	54	< 0,001
P ₂ -P ₄				KRM > GGW	23,50	1	0,05-0,02
M ₁ -M ₃				KRM > Hnv	13,53	2	0,005
He > Hn	4,28	80	< 0,001	HORN-CORE BASES			
He > Hnv	2,20	31	0,035	Medio-lateral diameter (all ages for He and Hn)			

	t	df	p		t	df	p
dP ₂ MW	2.46	13	0.029	dP ₄ NW	6.67	2	0.022
He > Hn	5.55	2	0.031	He > KRM			
NBC > LP				dP ₄ MW	2.72	12	0.019
dP ₃ NW	2.89	8	0.020	He > Hn	2.36	10	0.040
He > KRM	2.83	13	0.014	He > KRM			
NBC > KRM	2.45	11	0.032	dP ₄ LW	5.47	33	< 0.001
NBC > ZW				He > Hn	2.85	24	0.009
dP ₃ MW	4.87	3	0.017	He > UND	2.35	16	0.032
He > Hn	5.47	4	0.005	HeFF > HeMM			
He > ZW	2.67	5	0.044	P ₂ EW	4.88	46	< 0.001
He > NBC				He > Hn	2.89	17	0.010
dP ₃ LW	4.86	24	< 0.001	He > KRM	2.75	8	0.025
He > Hn	2.42	21	0.025	HeMM > HeFF	2.93	40	0.006
He > KRM	3.32	7	0.013	NBC > Hn			
NBC > Hn	3.70	4	0.021	P ₂ MW	2.42	11	0.034
NBC > KRM				He > Hn	2.76	10	0.020
dP ₄ MW	2.76	12	0.017	KRM > Hn			
He > Hn	5.90	3	0.010	P ₃ EW	10.34	55	< 0.001
KRM > Hn	6.54	4	0.003	He > Hn	3.55	27	0.001
NBC > Hn				He > KRM	3.07	27	0.005
dP ₄ LW	3.74	27	0.001	He > ZW	2.65	41	0.011
He > Hn	2.47	23	0.021	He > NBC	2.10	25	0.046
He > KRM	2.34	13	0.036	He > Hnv	4.81	48	< 0.001
HeMM > HeFF				NBC > Hn	2.26	34	0.031
dP ₂ NW	16.29	2	0.004	ZW > Hn			
NBC > KRM				P ₃ MW	3.44	3	0.041
dP ₂ MW	3.08	9	0.013	NBC > HTN			
He > KRM	2.37	7	0.049	P ₃ LW	5.06	10	< 0.001
He > Hn				He > Hn	2.60	5	0.048
dP ₂ LW	5.51	34	< 0.001	NBC > He	4.59	5	0.006
He > Hn				NBC > Hn	3.46	5	0.018
dP ₃ EW	2.98	4	0.041	UND > Hn	2.77	5	0.039
He > Hn				MHB > Hn			
dP ₃ LW	4.89	32	< 0.001	P ₄ NW			
He > Hn				He > Hn	4.60	5	0.006

	t	df	p		t	df	p
P ₁ EW	9,97	54	< 0,001	M ₁ LW	3,24	26	0,003
He > Hn	2,31	28	0,029	He > Hn	4,52	4	0,011
He > KRM	4,24	32	< 0,001	HeFF > HeMM	2,21	18	0,041
ZW > Hn	3,52	34	< 0,001	Hnv > Hn	2,28	24	0,032
KRM > Hn	4,48	31	< 0,001	KRM > Hn	2,77	19	0,012
NBC > Hn	2,73	5	0,041	NBC > Hn			
NBC > KRM				M ₃ NW			
P ₄ MW	5,84	19	< 0,001	He > KRM	6,27	14	< 0,001
He > Hn	2,99	5	0,031	He > EFT	2,63	12	0,022
He > Hnv	3,43	5	0,019	M ₃ EW			
He > KRM	7,80	2	0,016	He > Hn	5,68	29	< 0,001
ZW > Hnv	10,75	2	0,009	He > KRM	5,78	17	< 0,001
ZW > KRM	4,58	16	< 0,001	He > EFT	5,09	12	< 0,001
ZW > Hn	3,03	15	0,008	OAK > He	3,12	11	0,010
EFT > Hn	3,00	16	0,008	OAK > Hn	3,90	18	0,001
BMB > Hn				OAK > KRM	4,32	6	0,005
P ₄ LW	6,83	15	< 0,001	M ₂ MW			
He > Hn	3,76	9	0,005	He > Hn	10,69	76	< 0,001
He > KRM	2,69	8	0,028	He > ZW	6,17	37	< 0,001
He > NBC				He > KRM	3,87	45	< 0,001
M ₁ NW	3,39	8	0,009	He > EFT	6,54	36	< 0,001
ZW > KRM	2,71	8	0,027	He > BMB	2,72	33	0,010
UND > KRM				He > EC	4,44	33	< 0,001
M ₁ EW	2,83	13	0,014	He > NBC	3,55	40	0,001
He > Hn	2,19	13	0,047	KRM > Hn	2,07	55	0,043
He > KRM	2,46	15	0,026	ZW > EFT	2,72	7	0,030
NBC > He	4,16	8	0,003	OAK > EFT	3,35	3	0,044
NBC > Hn	3,60	8	0,007	MHB > EFT	11,23	4	< 0,001
NBC > KRM				MHB > ZW	22,73	5	< 0,001
M ₁ MW	10,84	91	< 0,001	MHB > NBC	2,34	8	0,047
He > Hn	6,11	56	< 0,001	MHB > Hnv	5,43	2	0,032
He > KRM	3,60	48	0,001	NBC > Hn	2,41	50	0,020
He > EFT	4,94	49	< 0,001	BMB > EFT	4,05	4	0,015
He > ZW	3,55	56	0,001	Hnv > Hn	2,43	44	0,019
He > NBC	3,34	59	0,001	Hnv > EFT	2,84	4	0,001

	t	df	p		t	df	p
P ¹ LW				He > EFT			
He > Hn	5,24	21	< 0,001	CS > KRM	4,04	11	0,002
ZW > Hn	2,89	11	0,015	CS > EFT	6,74	4	0,003
KRM > Hn	3,96	10	0,003		12,59	1	0,050
NBC > Hn	4,93	11	< 0,001	M ² EW			
NBC > He	2,24	12	0,045	He > Hn	2,28	29	0,030
UND > Hn	4,18	10	0,002	He > KRM	2,98	18	0,008
UND > He	2,37	11	0,010	He > NBC	4,67	23	< 0,001
M ¹ EW				He > EFT	2,76	18	0,013
He > KRM	3,00	13	0,010	Hn > KRM	2,51	13	0,026
He > Hn	2,49	11	0,030	Hn > NBC	3,33	18	0,004
He > EFT	2,27	10	0,047	Hn > EFT	2,20	13	0,046
M ¹ MW				CS > NBC	3,11	6	0,021
He > Hn	11,70	11	< 0,001	CS > Hn	2,27	12	0,043
He > KRM	6,03	69	< 0,001	M ² MW			
He > HTN	3,34	62	0,001	He > Hn	6,93	105	< 0,001
He > EFT	2,22	62	0,030	He > ZW	3,26	52	0,002
NBC > Hn	4,05	58	< 0,001	He > KRM	7,26	61	< 0,001
NBC > KRM	2,20	16	0,043	Hn > KRM	3,17	64	0,002
UND > Hn	5,01	50	< 0,001	Hnv > Hn	2,51	55	0,015
UND > KRM	4,46	8	0,002	Hnv > ZW	9,62	2	0,011
M ¹ LW				M ² LW			
He > Hn	2,63	40	0,012	He > Hn	5,35	11	< 0,001
HnMM > HnFF	3,62	15	0,003	NBC > Hn	2,87	4	0,045
Hnv > Hn	2,74	21	0,012	MHB > Hn	2,96	4	0,042
ZW > Hn	3,14	21	0,005	M ³ NW			
NBC > He	3,40	24	0,002	He > KRM	5,69	8	< 0,001
NBC > Hn	4,63	24	< 0,001	Hn > KRM	10,39	7	< 0,001
NBC > KRM	2,75	11	0,019	ZW > KRM	13,40	3	< 0,001
KRM > Hn	2,19	27	0,037	NBC > KRM	19,74	4	< 0,001
MHB > He	2,86	20	0,010	NBC > Hn	3,45	5	0,017
MHB > Hn	3,29	20	0,004	M ³ EW			
MHB > KRM	2,75	7	0,029	He > KRM	3,31	33	0,002
M ² NW				He > NBC	2,70	25	0,012
He > KRM	6,44	14	< 0,001	Hn > KRM	4,12	28	< 0,001

M ³ MW	t	df	p	Hnv > Hn	t	df	p
He > Hn	4,45	66	< 0,001	Hnv > Hn	5,16	34	< 0,001
He > KRM	6,63	39	< 0,001	Hnv > ZW	15,88	1	0,040
He > EFT	2,57	34	0,015	Hnv > NBC	5,64	5	0,002
He > ZW	2,28	33	0,029	Hnv > KRM	9,92	7	< 0,001
He > Hnv	3,99	34	< 0,001	Hnv > EFT	4,72	2	0,043
Hn > KRM	3,57	39	0,001	NBC > KRM	5,95	10	< 0,001
				NBC > ZW	2,86	4	0,046